Beyond the pond: terrestrial habitat use by frogs in a changing climate.

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Abstract

Amphibians are proportionately over-represented in the current wave of global biodiversity loss. Disease and habitat loss are implicated in many amphibian species declines, but amphibians are also predicted to be sensitive to changes in climate, particularly changes in temperature and loss of moisture. These changes could severely impact frog use of terrestrial habitats. We used data from a long-term (2007-18) landscape-scale experiment in south-eastern Australia to test the effects of terrestrial habitat characteristics and restoration treatments on frog species. We found declines in species richness and in the occurrences of two locally-common species (*Limnodynastes tasmaniensis* and *Uperoleia laevigata*). These declines were associated with high maximum temperatures, low minimum temperatures and low rainfall. Coarse woody debris addition was associated with higher species richness and *L. tasmaniensis* occurrence, but this effect was not greater in times of reduced rainfall and high maximum temperatures, implying a weak 'refugia' effect. Frogs were positively associated with wetter sites, and this association increased with higher maximum temperatures. Our findings add to a growing body of evidence that show that prolonged periods of drought pose a key threat to frog populations and that short periods of relief from drought conditions are insufficient to allow recovery of terrestrial frog populations over the long term. Restoration efforts could include the provision of coarse woody debris and should also ensure that good quality aquatic habitat, such as drought-resistant ponds and dams, are available throughout hot and dry times as a supplement to ephemeral aquatic habitat.

Introduction

The current human-caused global wave of biodiversity loss has led to the suggestion that we are in the midst of the sixth mass extinction event in Earth's history (Wake and Vredenburg 2008, Ceballos et al. 2015). Among those most impacted are amphibians, which are declining at an alarming rate (Stuart et al. 2004). Amphibians are impacted by several interacting and compounding factors, including disease (Scheele et al. 2019), habitat loss and fragmentation

(Cushman 2006) and may be particularly vulnerable to changes in climate (Hof et al. 2011, Miller et al. 2018). They are ectothermic, and many species have narrow climate niches (Bonetti and Wiens 2014), having low tolerances to changes in temperature and loss of moisture (Nowakowski et al. 2018). This is thought particularly the case for subtropical and tropical species, with those in temperate climes having a relatively high tolerance for changes in temperature (Duarte et al. 2012), at the expense of being more dependent on rainfall events to initiate breeding (Cohen et al. 2018). Further, amphibians are severely impacted by increased frequencies and lengths of drought (Mac Nally et al. 2014, fsd Mac Nally et al. 2017) where drying up of their aquatic breeding habitat impacts the long-term viability of the population (Rowe and Dunson 1995, Semlitsch et al. 1996, Ryan 2007).

Most research on amphibian populations is based on survey data acquired from aquatic breeding habitat. Amphibian occurrences and population trends, however, are also strongly influenced by terrestrial habitat features (Denton et al. 1997, Hazell 2003, Rittenhouse and Semlitsch 2007). Terrestrial habitat is crucial for overwintering in temperate regions (Lamoureux and Madison 1999) and its quality has fundamental implications for the maintenance of populations via metapopulation dynamics (Marsh and Trenham 2001). Amphibians use terrestrial habitat for movement through the landscape, and this habitat can act as a refuge when aquatic habitat is of unusually poor quality (Hazell et al. 2001, Westgate et al. 2018). Terrestrial microhabitat is also thought to play an important role in protecting frogs, and ectotherms in general, from unusually hot or dry conditions (Scheffers et al. 2014, Sunday et al. 2014). The amount and quality of terrestrial habitat, therefore, is likely to be an important factor shaping amphibian responses to climate change (Shoo et al. 2011).

Movement through terrestrial environments, including dispersal between aquatic habitats, can be physiologically challenging for amphibians. Away from water, amphibians are at risk of desiccation and the sites that they choose to occupy are likely to contain elements that reduce this risk. This could be especially true in times when the climate is unusually dry or hot for longer periods, as is expected to occur in future due to climate change. For example, logs and other woody debris, which are known to provide refuges for amphibians (Stewart 1995, Rittenhouse et al. 2008, Indermaur and Schmidt 2011), might also aid persistence under changing climate conditions. Whether these habitat characteristics can mitigate against the negative effects of temporal climate change on amphibians, however, has rarely been tested.

We used long-term data collected at the Mulligans Flat-Goorooyarroo Woodland Experiment (MFGOWE) in south-eastern Australia (Manning et al. 2011, Shorthouse et al. 2012) to test the effects of several terrestrial habitat characteristics and restoration treatments on frog species experiencing changes in climate. The MFGOWE was established to test the ecosystem effects of several restoration treatments, including coarse woody debris addition (CWD) and native vertebrate grazing reduction. As part of the MFGOWE, we monitored frog occurrences in terrestrial habitat over 12 years. We examined patterns of terrestrial habitat use by frogs through time, in response to treatments, and whether certain habitat elements are used more in times when the climate is unfavourable for frogs (e.g. in droughts). Using data collected from 2007 to 2018 during times of severe drought (before mid 2010, 2017 onwards) with temporary reprieves of wet and cooler weather (2010-2012, 2016), we asked the following questions:

Q1. What are the long-term trends of terrestrial habitat use by frogs?

Q2. What climatic factors are associated with these trends?

Q3. Which terrestrial habitat elements influence frog responses to unfavourable weather?

Methods

EXPERIMENTAL DESIGN

The MFGOWE comprises of two companion experiments located within the Mulligans Flat (791 ha) and Goorooyarroo (703 ha) nature reserves in south-eastern Australia (Fig. 1). The reserves consist of yellow box (*Eucalyptus melliodora*) – Blakely's red gum (*Eucalyptus blakelyi*) grassy woodland (hereafter referred to as box-gum grassy woodland), which is nationally listed as a 'Critically Endangered Ecological Community' (Department of Environment 2017). Combined, the experiments consist of 96 one-hectare sites (50 x 200 m) grouped within 24 polygons (Fig. S1). The experiments were designed to test the effects of restoration treatments such as coarse woody debris addition and reduced grazing (Table 1). Sites were also distributed across different categories of vegetation structure and cover, allowing several more environmental variables to be tested (Table 1). Sites do not overlap and are oriented to capture a range of slopes, topography and aspects. Mulligans Flat is surrounded by a fence designed to exclude feral predators such as the fox (*Vulpes vulpes)* and cat (*Felis catus*) (Shorthouse et al. 2012).

FROG SURVEYS

We used data on frogs collected concurrently with reptile surveys outlined in other research (Manning et al. 2013, Evans et al. 2019). Briefly, we conducted surveys in every 1 ha site twice per year (March or April) from 2007 to 2018, with the exception of 2009 when were unable to survey sites in Mulligans Flat because of wet and overcast weather. We surveyed all polygons in random order which was reversed in the second set of yearly surveys. We searched all substrates within each site carefully, including logs, rocks and bark. To reduce bias towards searching particular substrates, we allocated an equal time of 7.5 minutes search time for each 0.25 ha (50 m x 50 m) segment within each site. We assumed that detection was constant but acknowledge that perfect detection may not be possible. For example, frogs may be harder to detect during dry periods (Valenzuela-Sánchez et al. 2019).

ANALYSIS

Data preparation

In previous research conducted at the MFGOWE, data collected in each reserve have been analysed separately (e.g. Manning et al. 2013, Evans et al. 2019). This is due to the differing management histories and vegetation of the two reserves and because each experiment has been designed with internal validity in mind, with appropriate randomisation, replication and controls. We maintained this approach here but have also opted to provide overall effects with all the data combined into one analysis to aid in the interpretation of the results. This has resulted in three analyses per model set – one for Mulligans Flat, one for Goorooyarroo and one for them combined. Sdfad

Response variables

Our response variables were the occurrences of the two most common species detected in the surveys: *Limnodynastes tasmaniensis* and *Uperoleia laevigata* (Table1). For completeness and to provide an indication of other species detected, we also analysed overall species richness at the site level.

Predictor variables

Our predictor variables consist of variables associated with the restoration experiment, variables associated with environmental variation between the sites and variables that vary through the time of the experiment (Table 1). For further details on many of these variables, including their justifications and details on their implementations, see Shorthouse et al. (2012) and Evans et al. (2019). To enable comparisons between the effects of all the predictors, we rescaled all continuous predictor variables to have a mean of zero and a standard deviation of one.

Time

To determine the trends of frog richness and occupancies of species through time, we used the year of survey as a predictor variable (Table 1).

Climate variables

To test the effects of climate on frogs through the time of the experiment, we calculated three climate variables: mean maximum temperature, mean minimum temperature and mean daily rainfall for the four months preceding the survey period each year (Table 1). We calculated each variable by using estimated means from linear models of daily observations collected at local weather stations downloaded from the Australian Bureau of Meteorology website (Bureau of Meteorology 2019). We modelled these daily observations against year factors (e.g. *daily rainfall ~ year as a factor*). For this analysis, we used rainfall observations for January until April and year-round observations of temperature. This gave us one value per year for each variable.

Coarse woody debris addition

The first of the restoration experiment variables is the addition of coarse woody debris (CWD) to 72 of the sites. In October 2007, a total of 2000 tonnes of CWD was added to the sites in three configurations: 20 tonnes per site in a *dispersed* arrangement, 20 tonnes per site in a *clumped* arrangement, and 40 tonnes in a *combined* arrangement of both dispersed and clumped CWD. These categories of additions were arranged so that each polygon had sites with all three categories plus a site with no added CWD which acted as a *control.* Frog surveys in 2007 were conducted before the addition of CWD, therefore, for the purposes of the analyses we coded all sites as ‘control’ in this year.

Grazing reduction

To test the effects of grazing pressure reduction, kangaroo exclusion treatments were applied to half of the polygons in Gooroyarroo in 2007 and half of the polygons in Mulligans Flat in early 2010 (Fig. 1c). The exclusion fences were designed to reduce the grazing pressure from the eastern grey kangaroo (*Macropus giganteus*), the dominant large native herbivore in the reserves. The grazing treatments should be considered as two levels (‘low’ and ‘high’), owing to the fact that we were unable to completely exclude all kangaroos from within the exclosures. We classified all sites prior to the implementation of the treatment as ‘high’ grazing.

Vegetation class

Polygons within the experiments were classified into four broad vegetation structural classes reflecting their vegetation densities (Table 1). These include High Tree Cover with High Shrub Cover (HTHS), High Tree Cover with Low Shrub Cover (HTLS), Low Tree Cover with High Shrub Cover (LTHS) and Low Tree Cover with Low Shrub Cover (LTLS). The number of polygons assigned to HTHS, HTLS, LTHS and LTLS is 4, 3, 0, 5 and 4, 1, 5, 2 in Goorooyarroo and Mulligans Flat, respectively (Table S1).

Distance to water

Mulligans Flat and Goorooyarroo both contain several permanent water bodies, most of which are artificial dams. Many frog species in the reserves are known to use these as breeding sites. To determine whether distance to permanent water affected site occupancy, we measured the distance in metres from the centre of each site to the edge of the nearest permanent water body using ArcGIS.

Wetness

To test whether moisture affects frog occurrence, we calculated two metrics of wetness for each site: site wetness and surrounding wetness (Table 1). The site metric of wetness was designed to test the effects of site wetness as a refuge for frogs, whereas the surrounding wetness was designed to test whether increased moisture in the surrounding landscape is associated with frog occupancy. We quantified wetness using the topographical wetness index (TWI) derived from a digital elevation model (DEM) of the experimental area. We calculated the TWI following Beven and Kirkby (1979):

$$TWI = ln\left(\frac{A_s}{tan\beta}\right) \quad (1)$$

Where β represents slope angle in radians and A_s is the specific catchment area (m^2 m^{-1}). Specific catchment area was calculated using methods described by Gallant and Hutchinson (2011) as the upslope contributing area (A, m^2) per unit contour length (w, m):

$$A_S = \frac{A}{w} \qquad (2)$$

We derived A using the M8 multiple flow direction router tool available in the Python-based Landlab landscape modelling package (Hobley et al. 2017) and w was given by:

$$w = \begin{cases} R,\ cardinals \\ \sqrt{2}.R,\ diagonals \end{cases} \qquad (3)$$

Where R is the working grid cell resolution (1 m). Prior to routing flow, the DEM was filled using the Priority-Flood depression filling algorithm (Barnes et al. 2014) implemented in the Landlab modelling package. The M8 method was preferred over a steepest downhill direction method (e.g. D8) to better represent the dispersive nature of flow on hillslopes and in flatter areas where a D8 algorithm can produce unrealistic concentrated flow lines (Desmet and Govers 1996, Seibert and McGlynn 2007).

From TWI, we calculated mean values of TWI for each 1 ha site and mean values of TWI for an area of 200 metres radius surrounding the site as indicator of site wetness and surrounding wetness, respectively using ArcGIS.

Research Questions.

Q1.What are the long-term trends of terrestrial habitat use by frogs?

To test the trends of frog terrestrial habitat use (frog richness and the two frog species occurrences) through the time of the experiment, we fitted both generalised additive mixed models (GAMMs) and generalist linear mixed models (GLMMs) using year as our predictor variable. We used GLMMs to examine the linear trend over the time of the experiment (decline, increase, no change). We used the GAMMs to examine any non-linear trends over time, such as declines in periods of drought. To account for spatial and temporal correlation, we used site number nested within polygon as a random intercept factor (~ *polygon/site*). We assumed a Poisson error distribution with a log link for species richness, checking for overdispersion, and a binomial error distribution with a logit link for the individual species occurrence response variables.

Q2. What climatic factors are associated with these trends?

To test which factors were driving the trends shown in answering Question 1, we fitted a series of GLMMs of our response variables fitted to several predictor variables that vary through time, including maximum temperature, minimum temperate, rainfall and survey year. We fitted all subsets of the full model and performed model averaging on all models below ΔAICc=5 (Burnham and Anderson 2002, Anderson 2007). For each predictor variable, we then calculated the mean estimates and 95% confidence intervals for this subset of models. We interpreted variables as significant if their 95% confidence intervals did not cross the zero-effect line (du Prel et al. 2009, Welsh 2011). To account for spatial and temporal correlation, we used the same random effects described in Question 1, apart from when we combined the data from both experiments, where we used site nested within polygon nested within experiment as random effects (~ *experiment/polygon/site*). If any of the variables outcompeted the time variable, or reduced it to non-significance, we interpreted them as the factors behind any linear temporal trend.

Q3. Which terrestrial habitat elements influence frog responses to unfavourable weather?

To test whether frogs use certain terrestrial features more when the climate is hostile (as demonstrated in Question 1), we fitted GLMMs of the identified factors in Question 2 as variables interacting with habitat components against our response variables. We conducted the same model averaging procedure as used in Question 2 for five categories of habitat features: CWD addition, grazing reduction, distance to water, site wetness (including both site and surrounding wetness variables) and vegetation class. For example, if we found that maximum temperature was associated (Question 2) with declines (Question 1), we fitted the following five sets of models:

response ~ *time*maximum temperature + maximum temperature*CWD addition*

response ~ *time*grazing reduction + maximum temperature*grazing reduction*

response ~ *time*distance to water + maximum temperature*distance to water*

response ~ *time*site wetness + time*surrounding wetness +*
*maximum temperature*site wetness +*
*maximum temperature*surrounding wetness*

response ~ *time*veg class + maximum temperature*veg class*

where an asterisk denotes the main effects plus the interaction (i.e. a*b = a+b+a:b). As with Question 2, we fitted all subsets of the full models listed above and performed model averaging on all models below ΔAICc=5, calculating the mean estimates and 95% confidence intervals for these subsets of models. To account for spatial and temporal correlation, we used the same random effects described in Question 2. We used interactive effects here to test whether there were differential effects of habitat components to changes in the mechanisms discovered in Question 2. For example, we may discover that as temperature increases, frogs are more likely to use CWD. This would be represented by a positive interactive effect of maximum temperature and CWD addition.

We used the ‘lme4’ (Bates et al. 2016), ‘gamm4’ (Wood 2017), ‘RVAideMemoire’ (Hervé 2019), ‘plyr’ (Wickham 2011), ‘gtools’ (Warnes et al. 2018), ‘forcats’ (Wickham 2018), ‘MuMIn’ (Barton 2016), ‘AICcmodavg’ (Mazerolle 2019), ‘ggplot2’ (Wickham 2009), and ‘ggpubr’ (Kassambara 2018) packages in R version 3.5.1. (R Core Team 2017) for all analyses and plotting.

Results

Over the time of the experiment we observed frogs 732 and 327 times in Mulligans Flat and Goorooyarroo respectively (Table 2). The most common species were *Limnodynastes tasmaniensis* and *Uperoleia laevigata,* with fewer occurrences of *Crinia signifera, Litoria peronii, Crinia parinsignifera, Litoria verreauxii* and *Limnodynastes peronii* (occurring only once).

Q1. What are the long-term trends of terrestrial habitat use by frogs?

Frog species richness showed a general decline in terrestrial habitat use in both reserves over the time of the experiment (Fig. 2). The GAMMs show similar trends in both reserves, with large increases in richness around 2010-2012 followed by a decline to 2018. There wasa smaller increase in richness in 2014 in Mulligans Flat. The occurrences of both *L. tasmaniensis* and *U. laevigata* showed similar trends to species richness, apart from demonstrating no linear trend for *L. tasmaniensis* in Goorooyarroo.

Q2. What climatic factors are associated with these trends?

Several factors were associated with declines in frog richness and occurrences, but none completely explained the linear declines over time described above (Fig. 3). Increased frog species richness was associated with lower maximum temperatures, higher minimum temperatures and increased rainfall. In other words, hotter maximum temperatures, colder minimum temperatures and decreased rainfall (conditions which characterize drought periods in our study region) all contributed to frog declines. Species richness in both reserves combined, however, was shown to decline even when maximum temperature, minimum temperature and rainfall were accounted for. Patterns of occurrences for *L. tasmaniensis* and *U. laevigata* were similar to those of species richness, with the exception that maximum temperature did not explain occurrences of *L. tasmaniensis.*

Q3. Which terrestrial habitat elements influence frog responses to unfavourable weather?

Coarse woody debris addition

Whilst species richness and occurrences of *L. tasmaniensis* increased in all CWD addition treatments (Fig. 4), there were no significant interactive effects of CWD addition and any of the climate variables or time. The interactions of CWD addition and maximum temperature appeared in the highest-ranked models for *U. laevigata* occurrence, but their confident intervals overlapped zero (Fig. S2). The interactions of CWD addition and minimum temperature appeared in the highest-ranked models for *L. tasmaniensis* occurrence in Mulligans Flat, but their effect sizes were not significant (Fig. S3). These patterns indicate that although frogs were associated with CWD, they did not use them more when the climate was hostile.

Grazing reduction

Reduced grazing showed interactive effects over time for species richness and *U. laevigata* (Fig. 5). More specifically, grazing reduction resulted in an increase in species richness and *U. laevigata* occurrence, but only in the earlier years (Fig. 5A and 5B). In Mulligans Flat only, species richness increased in sites of reduced grazing when the maximum temperature was higher (Fig. 5C).

Vegetation

Sites with high tree and low shrub cover had lower decreases in species richness in both reserves when maximum temperatures were high (Fig. 6A). *L. tasmaniensis* occurrences showed a similar pattern in Mulligans Flat with increases in occurrences in high tree, low shrub sites as maximum temperatures increased whilst other sites simultaneously demonstrated decreases as maximum temperatures increased (Fig. 6B).

Distance to water

Species richness and *L. tasmaniensis* occurrence were lower in sites further away from permanent water bodies, but these effects were only significant when using Mulligans Flat and Goorooyarroo data combined (Fig. 7). *U. laevigata* occurrence showed an interactive negative effect with distance to water and maximum temperature, but only in Mulligans Flat (Fig. S5).

Wetness

L. tasmaniensis demonstrated a reduction in occurrence in wetter sites as time increased (Fig. 8A). An increase in site wetness resulted in an increase in species richness, which increased as maximum temperature increased, as shown by the interactive effect (Fig. 8B). Site wetness also increased *U. laevigata* occurrence, but only when the maximum temperature was high (Fig. 8C). Surrounding wetness had very few significant effects apart from an increase in *L. tasmaniensis* occurrences in sites with wetter surrounds when the maximum temperature increased.

Discussion

From 2007 to 2018, the occurrence of frogs in terrestrial habitat in our box-gum grassy woodland experiment declined. While caution is needed in linking declines in occurrences in terrestrial habitat to absolute population numbers in the landscape, our findings are concerning. If we assume that frogs need terrestrial habitat for persistence (i.e. for migration, metapopulation persistence, refuges), then reduced occurrences might indicate that frog populations are in decline. They might also indicate, however, that frogs have moved to alternative habitat such as a permanent water source. The declines were associated with unfavourable climate conditions, including higher daily maximum temperatures, lower daily minimum temperatures and decreased rainfall. Furthermore, negative responses to decreased rainfall and increased temperature do not seem to be mitigated by restoration efforts such as CWD addition and reduced grazing – i.e. frogs do not use these habitat elements more when the climate is more hostile.

THE IMPACTS OF A CHANGING CLIMATE

Reductions in frog occurrences in our study were associated with increased maximum temperatures, decreased minimum temperatures and reduced rainfall. When frogs are away from their aquatic habitat, they are at considerable risk of desiccation (Tracy et al. 2010), so it is expected that their movement through the landscape, and hence terrestrial habitat use, increases under moister conditions. Our finding that frogs were associated with wetter sites during high maximum temperatures is also consistent with this, suggesting that the frogs seek moisture during hot spells, possibly even switching to wetter microhabitats as temperatures rise. As a result of climate change, southern Australia is expected to experience increases in average temperatures, more hot days, decreases in rainfall and increases in the intensity and frequency of extreme weather events, such as droughts (Suppiah et al. 2007, Prudhomme et al. 2014, CSIRO and Bureau of Meteorology 2019). Our results suggest that within a given landscape, sites with more moisture will become crucial for the survival of frogs in the future, potentially acting as refuges.

The long-term trends we report are consistent with other research in south-eastern Australia. Prolonged droughts have severe impacts on the distribution (Mac Nally et al. 2009), abundances, occurrences and breeding of frogs (Cayuela et al. 2016, Mac Nally et al. 2017). Our results also concur with evidence suggesting that temporary reprieves from dry and hot weather provided by short periods of wet weather (3-9 months) are insufficient to allow recovery of frog populations over the long term (Mac Nally et al. 2014, Mac Nally et al. 2017). We speculate that the key negative impact of drought is through increased temperatures and decreased rainfall resulting in premature drying up of aquatic habitat such as ponds, especially over successive years. This can lead to tadpole mortality and reduced metamorphic success which impacts frog recruitment and the long-term viability of the population (Rowe and Dunson 1995, Semlitsch et al. 1996, Ryan 2007, Stevens and Baguette

2008). Reduced recruitment is particularly important in species impacted by chytridiomycosis, which in some cases are highly dependent on recruitment to offset elevated rates of adult mortality (Scheele et al. 2016). Additionally, adult mortality in terrestrial environments is likely to increase under periods of extreme drought stress and high temperatures. Our results, alongside other research from southern Australia indicates that drought-associated declines are occurring in common, generalist frog species (Mac Nally et al. 2014, Mac Nally et al. 2017), as well as specialist species with small ranges (Scheele et al. 2012). Therefore, we predict that populations of many species will likely continue to decline, and frogs will contract to shrinking refugia in mesic parts of the landscape.

RESTORATION TREATMENTS

Our results suggest that, although frogs might use some of the terrestrial habitat features used for restoration, they do not increase their use when under pressure from extreme climatic conditions. Frogs, however, were positively associated with the CWD addition treatments suggesting that CWD offers critical terrestrial refuges in all weather conditions. This patterns concurs with findings from North America, where CWD was shown to reduce desiccation risk in clear-cut forests for three species of frogs (Rittenhouse et al. 2008). Further, findings from elsewhere in southern Australia suggest that *L. tasmaniensis* use logs as refuges (Pulsford et al. 2018). This species showed no response to increased maximum temperatures in our study, possibly indicating that its use of log habitat meant that it was less vulnerable to such increases. There was no indication, however, that frogs in our study used CWD more frequently as a refuge when temperatures were higher, or when rainfall was lower. This suggests that CWD addition, whilst providing habitat for species, may not help buffer against the negative effects of future climate change.

Frogs richness and *U. laevigata* demonstrated positive responses to reduced kangaroo grazing, but only in the early years of the study. Concurrently, frog richness increased in areas with reduced grazing when the maximum temperature was higher, but only in Mulligans Flat. These patterns might reveal that the increased vegetation structure resulting from reduced grazing helps movement and that this is especially true in times of hot weather. These results, however, do not entirely dovetail with other evidence on these species. For example, Pulsford et al. (2019) demonstrated that frogs, including *L. tasmaniensis,* were associated with taller ground cover in remnant vegetation but not in grazed paddocks (which have a very simple ground layer). They attributed this to greater predation risk in remnants than in grazed paddocks. Pulsford et al. (2018) also showed that *U. laevigata* was more likely to move through native vegetation remnants than agriculturally grazed paddocks. Our results, on the other hand, also showed positive associations with low tree and high shrub sites when compared with high tree and high shrub sites. One interpretation is that frogs increase their use of areas with vegetation structure that provides cool conditions during hot weather but prefer ground-layer habitat that allows them to move through landscapes freely.

IMPLICATIONS FOR RESTORATION AND THE MANAGEMENT OF FROGS

The declines in habitat use we have identified add to concerns regarding the future of frogs under a changing climate. Our results suggest that attempts to provide terrestrial habitat restoration do not provide habitat for frogs in the landscape that buffers against the negative effects of drought. This is concerning given that existing research demonstrates that dry periods are often associated with population declines, likely driven by a limited tolerance to desiccation and the reliance on water for the survival of larvae and increased success of reproduction (Banks et al. 1994, Ficetola and Maiorano 2016). The finding that frogs use CWD in all periods of weather, however, does offer some indication that this terrestrial feature increases frog occupancy in general. Provision of CWD, therefore, as with reptiles (Evans et al. 2019), might boost population numbers in general and be of benefit to terrestrial frog species over the long term.

If frogs avoid terrestrial habitat in times of hot and dry weather, as our results suggest, then restoration efforts need to ensure that good quality aquatic habitat is provided throughout hot and dry times. This might be achieved with techniques such as drought resistant ponds and dams, and could be supplemented with the provision of wetter areas in terrestrial habitat (Shoo et al. 2011). We express caution, however - it is not appropriate to replace all ephemeral aquatic habitat with permanent aquatic habitat. Altering pond hydroperiods might make habitat unsuitable for some species of frogs, or conversely more suitable for others (Wellborn et al. 1996). For example, permanent water sources that are colonised by fish can result in reduced recruitment or wetland avoidance, potentially driving population declines (Werner and McPeek 1994). If aquatic habitat management is an option, an appropriate goal is to ensure the availability of a diversity of pond hydroperiods across the landscape, with suitable intervening terrestrial habitat to facilitate dispersal (Petranka and Holbrook 2006).

Further research is needed to determine whether the patterns of decline in terrestrial habitat use we report reflect the absolute population abundance of frogs in the area. It is possible that the declines we document are not a true reflection of frog abundances. Instead, they may result from a reduced likelihood of observing frogs, i.e. our detections could be confounded with climate conditions. For example, in times of unusual heat or desiccation stress, frogs may retreat to areas outside of the study sites such as water bodies that maintain some water, or in places where they are more difficult to detect such as deep in soil. However, we note that Westgate et al. (2015) reported declines of *L. tasmaniensis* and *U. laevigata* from rural areas and areas with low tree cover during the period 2002 to 2014 based on aquatic habitat surveys during the breeding season.

Despite uncertainty on whether the declines we report reflect population-level declines, our results should be of concern. The species in our study have previously been considered robust, being both apparently resistant to chytrid fungus, which is now endemic in our study region (Scheele et al. 2017), and able to persist in heavily modified urban and agricultural landscapes (Westgate et al. 2015). Yet their occupancy in terrestrial habitat changed considerably over 11 years. This could mean that these species are either in decline or have drastically changed the way that they use terrestrial habitat. Studies that monitor frogs in both terrestrial and aquatic habitats would help determine whether frogs have declined in absolute terms and would also provide crucial information of how frogs use the landscape in times of stress. This information will be of critical value in mitigating against the potential devastating impacts of climate change on frogs in south-eastern Australia and globally.

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Author contributions

MJE and ADM designed the methodology, MJE performed the analysis, conceived the ideas and led the writing of the manuscript; JSN, LR and MY collected the data and conceived the ideas; ADM leads the Mulligans Flat – Goorooyarroo Woodland Experiment and designed the overall experimental framework in collaboration with Ross Cunningham, Jeff Wood and David Lindenmayer (see Acknowledgements). ADM also collected the data and conceived the ideas. All authors contributed critically to the drafts and gave final approval for publication.

Ethics statement

All surveys were approved by ANU ethics.

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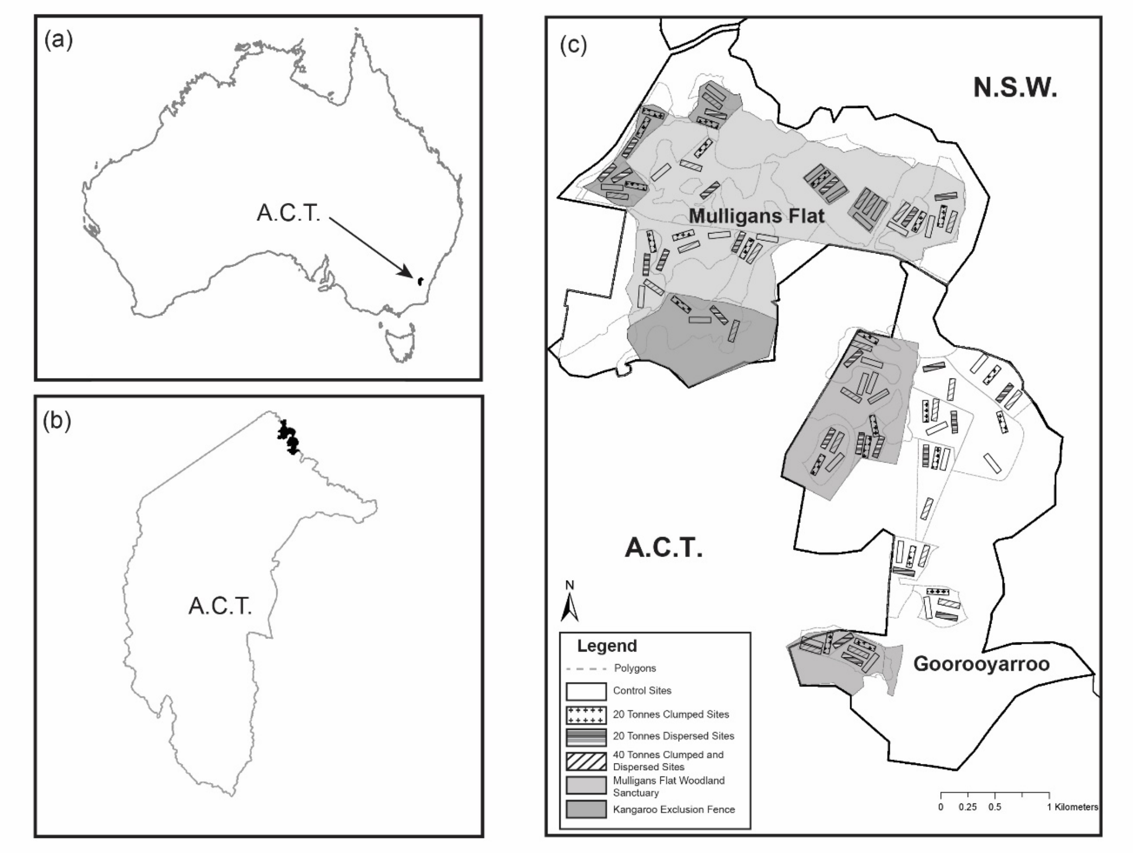
Table 1. Predictor variables used in analyses. All continuous variables were rescaled before analyses (mean = 0, SD = 1) except where stated. Q1, Q2 and Q3 columns signify in which questions the variables were analysed.

Name	Description	Category	Q1	Q2	Q3	Variation	Type	Details
Time	Year of survey.	Time	✓	✓	✓	Temporal	Continuous	Year of survey. 2007 to 2018 inclusive. Rescaled for some analyses.
Maximum temperature	Mean maximum daily temperature.	Climate		✓	✓	Temporal	Continuous	One value per year. Mean = 20.80˚C, Min = 19.93˚C, Max = 21.73˚C.
Minimum temperature	Mean minimum daily temperature.	Climate		✓	✓	Temporal	Continuous	One value per year. Mean = 7.12˚C, Min = 5.96˚C, Max = 7.92˚C.
Rain	Mean daily rainfall for 4 preceding months (Jan-April).	Climate		✓	✓	Temporal	Continuous	One value per year. Mean = 1.88mm, Min = 1.16mm, Max = 3.85mm.
CWD addition	Addition of coarse woody debris to 72 of 96 sites.	Terrestrial (Restoration experiment)			✓	Spatial	Factor	Four levels: 1. Control 2. Clumped (20 tonnes/site) 3. Dispersed (20 tonnes/site) 4. Combined (40 tonnes/site)
Grazing reduction	Polygons with kangaroos exclosures to reduce grazing pressure.	Terrestrial (Restoration experiment)			✓	Spatial	Factor	Two levels: 1. High grazing 2. Low grazing (kangaroo exclusion)
Veg class	Categories of vegetation class to represent vegetation densities in each polygon.	Terrestrial (Environmental variation)			✓	Spatial	Factor	Four levels: 1. High tree, high shrub 2. High tree, low shrub 3. Low tree, low shrub 4. Low tree, high shrub
Distance to water	Distance to nearest large water body.	Terrestrial (Environmental variation)			✓	Spatial	Continuous	One value per site. Mean = 281.79m, Min = 22.80m, Max = 646.47m
Site wetness	Topographical wetness index (site level).	Terrestrial (Environmental variation)			✓	Spatial	Continuous	One value of mean TWI per site.
Surrounding wetness	Topographical wetness index (within 200m buffer of site).	Terrestrial (Environmental variation)			✓	Spatial	Continuous	One value of mean surrounding TWI per site.

Table 2. Species of frogs detected during the experiment. Unbracketed numbers represent abundances and numbers in brackets represent occupancies of that species per site per year.

Species	Mulligans Flat	Goorooyarroo
Limnodynastes tasmaniensis	412 (142)	147 (70)
Uperoleia laevigata	212 (85)	140 (80)
Crinia signifera	59 (27)	18 (12)
Litoria peronii	13 (12)	16 (12)
Crinia parinsignifera	27 (14)	3 (3)
Litoria verreauxii	9 (8)	2 (2)
Limnodynastes peronii	0 (0)	1 (1)
Total	732	327



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703 **Fig. 1. Map of the Mulligans Flat and Goorooyarroo Nature Reserve study areas (c) and**
704 **their location in the Australian Capital Territory (b) in Australia (a).**

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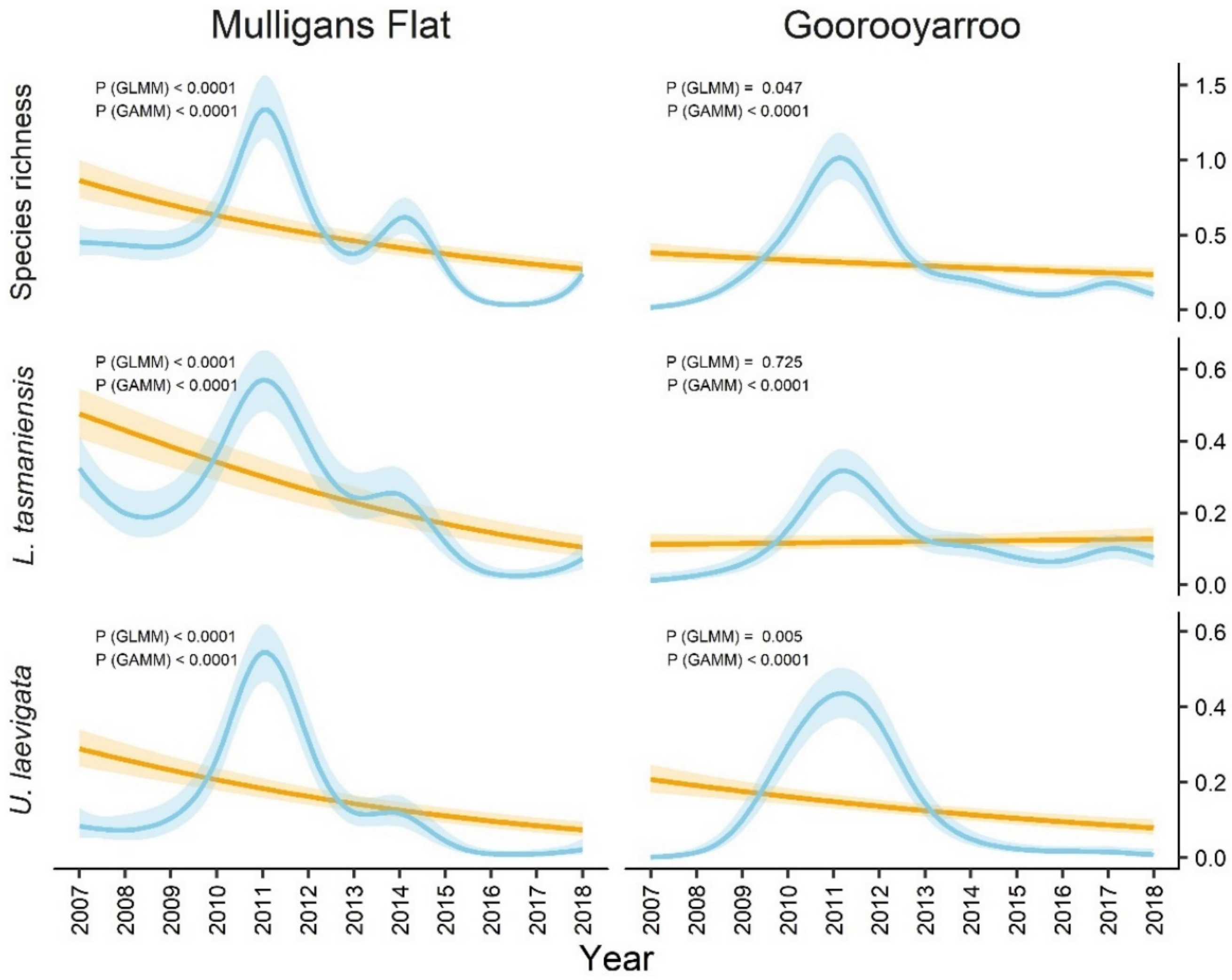

Fig 2. Predicted changes of species richness and species occupancy through time in both reserves. Y axes represent predicted species richness (top row) and probability of occurrence (middle and bottom rows). Predictions from GAMMs (blue) and GLMMs (yellow). Bands represent standard errors. P values represent the significance of the fits (< 0.05). Note the different scales on the y-axis. See Fig. S2 for effect size plots of the GLMMs.

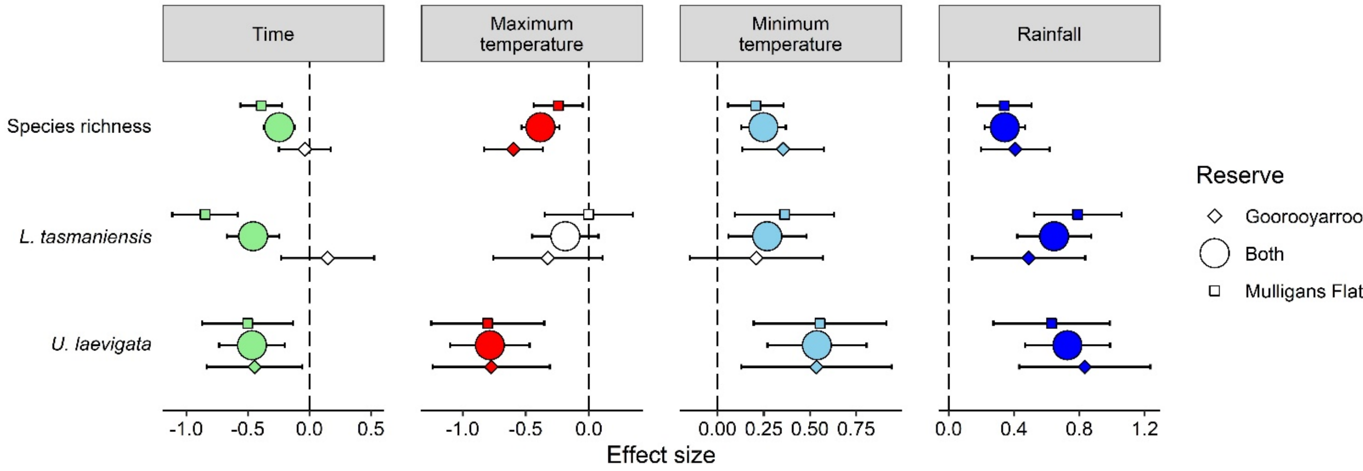

Fig. 3. Model-averaged coefficients (effect sizes) for all models below ΔAICc = 5 of all subsets of the following: *Response ~ time + maximum temperature + minimum temperature + (random effects).* All continuous variables were scaled to enable direct comparisons. Shaded symbols represent significant effects. Error bars represent 95% CIs.

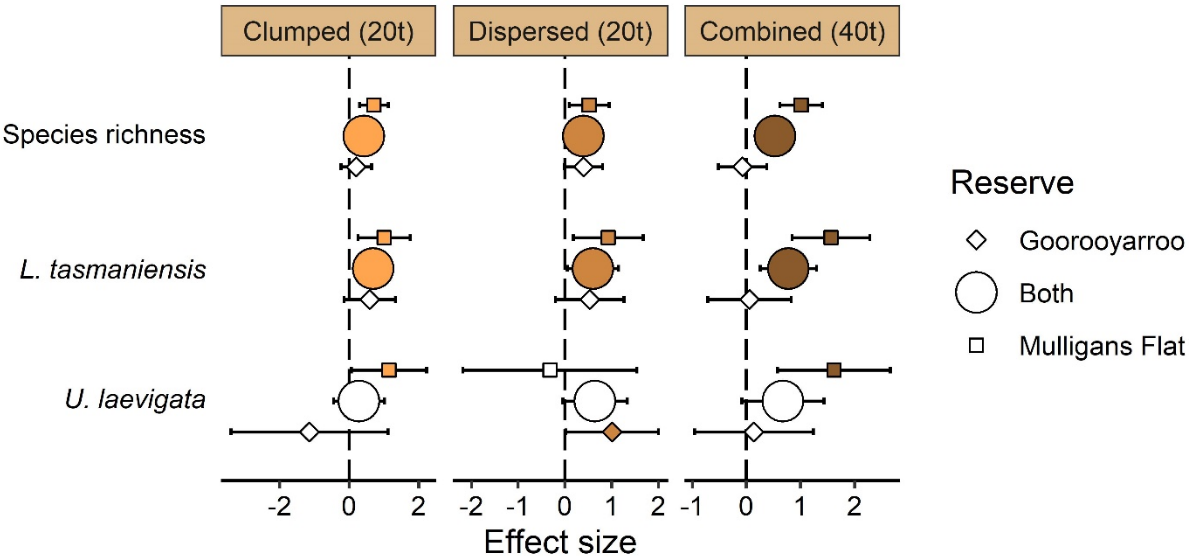

Fig. 4. Model-averaged model coefficients (effect sizes) for all models below ΔAICc = 5 of the top model of all subsets of the following model: *Response ~ time*CWD addition + rainfall*CWD addition + maximum temperature*CWD addition + minimum temperature*CWD addition + (random effects).* All continuous variables were scaled to enable direct comparisons. Coloured points represent significant effects. Error bars represent 95% CIs. Effect sizes of *time, maximum temperature, minimum temperature and rainfall* can be seen in Fig. S3. Interactive effect sizes were not significant so have been omitted from the figure (see Fig. S3).

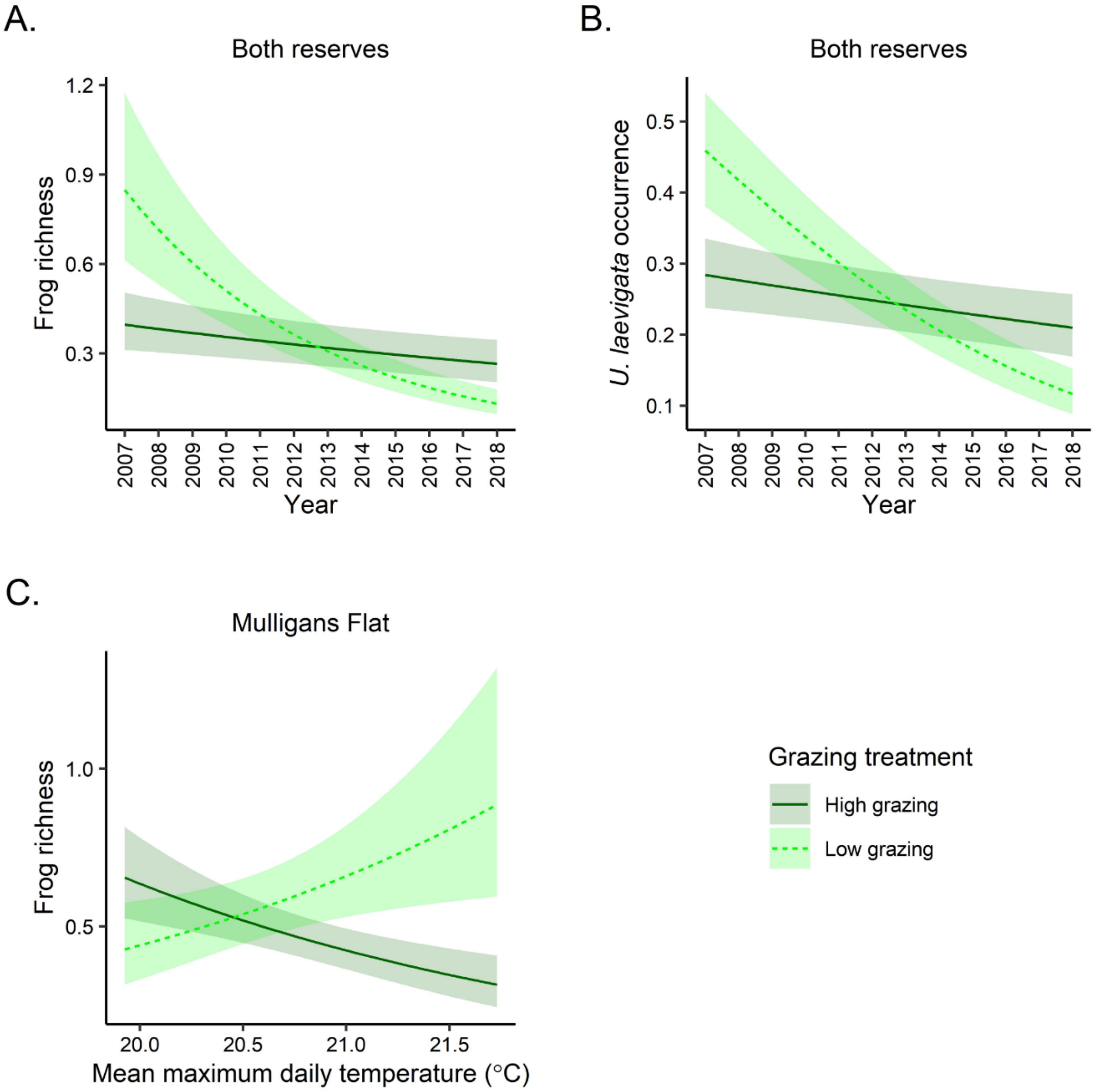

Fig. 5. Predicted trend plots for grazing treatment interactive variables that were significant in the model selection procedure. See Fig. S4 for model-averaged model coefficients (effect sizes) for all models within ΔAICc = 5 of the top model of all subsets of the following model: *Response ~ time*reduced grazing* + *rainfall*reduced grazing* + *maximum temperature*reduced grazing* + *minimum temperature*reduced grazing* + *(random effects)*. Shaded error bands represent standard errors.

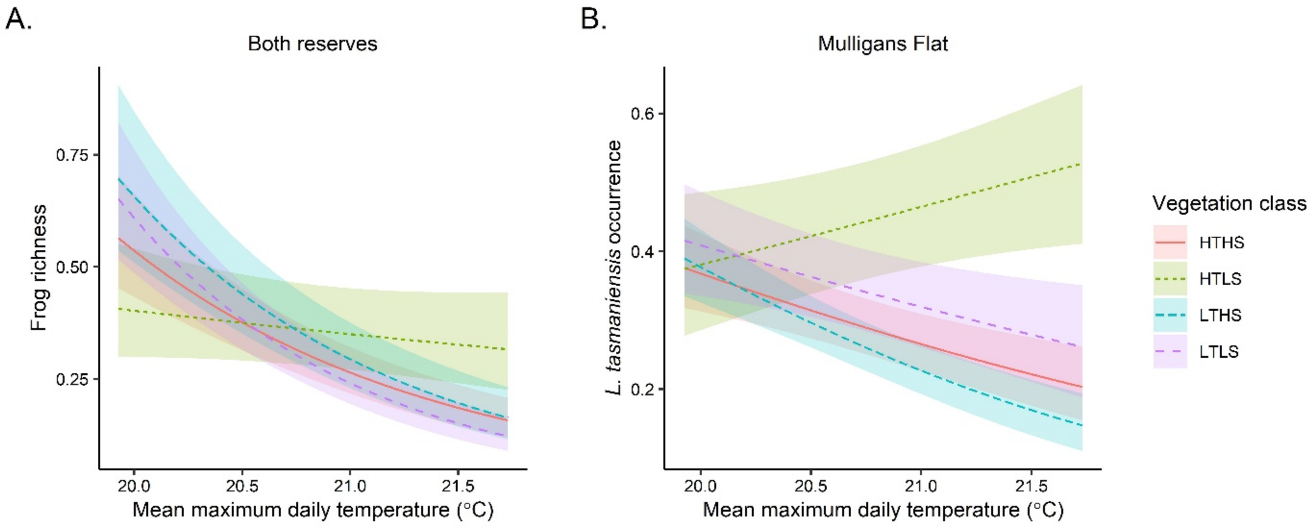

Fig. 6. Predicted trend plots for vegetation class interactive variables that were significant in the model selection procedure. See Fig. S5 model-averaged model coefficients (effect sizes) for all models within ΔAICc = 5 of the top model of all subsets of the following model: *Response ~ time*veg class + rainfall*veg class + maximum temperature*veg class + minimum temperature*veg class + (random effects).* Shaded error bands represent standard errors.

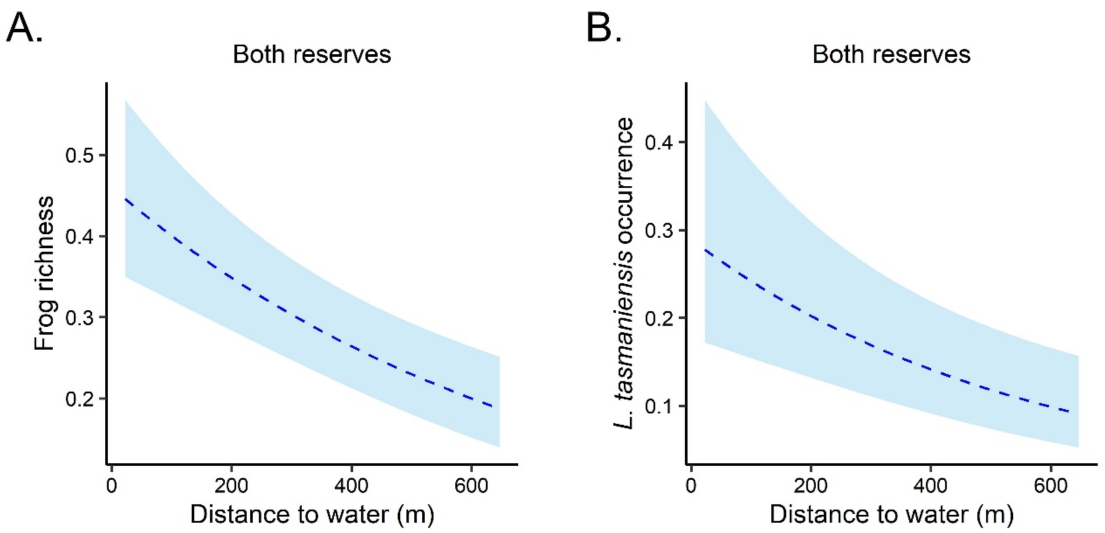

Fig. 7. Predicted trend plots for distance to water variables that were significant in the model selection procedure. See Fig. S6 for model-averaged model coefficients (effect sizes) for all models within ΔAICc = 5 of the top model of all subsets of the following model: *Response ~ time*distance to water + rainfall* distance to water + maximum temperature* distance to water + minimum temperature* distance to water + (random effects)*. Shaded error bands represent standard errors.

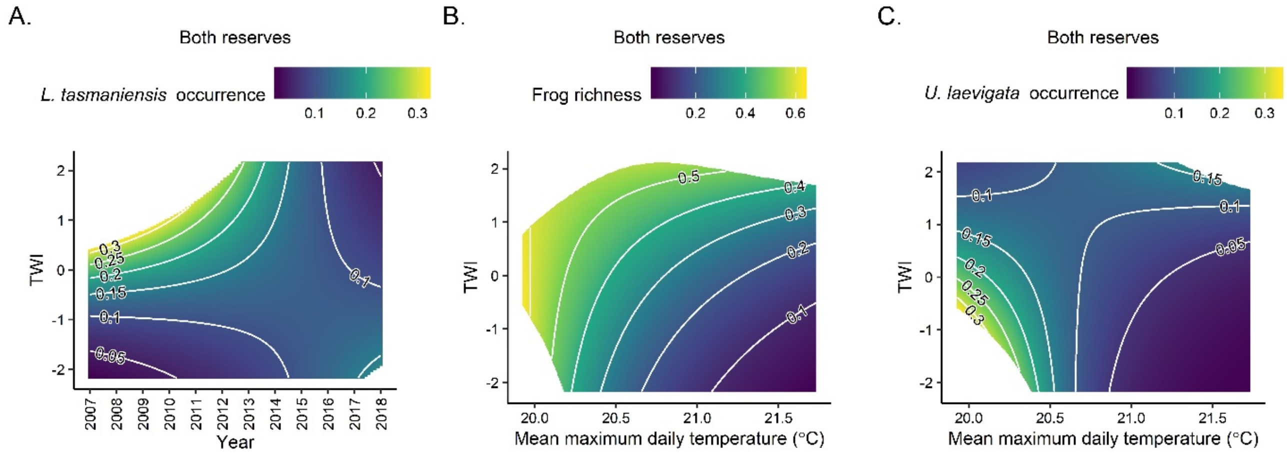

Fig. 8. Predicted surface plots for TWI treatment interactive variables that were significant in the model selection procedure. See Fig. S7 for model-averaged model coefficients (effect sizes) for all models below ΔAICc = 5 of the top model of all subsets of the following model: *Response ~ time*site wetness* + *rainfall*site wetness* + *maximum temperature*site wetness* + *minimum temperature*site wetness* + *time*surrounding wetness* + *rainfall*surrounding wetness* + *maximum temperature*surrounding wetness* + *minimum temperature*surrounding wetness* + *(random effects)*. White areas on the plot represent where the predicted values were not significant (p>0.05).